

A GRAPHICAL APPROACH TO A MODEL OF NEURONAL TREE WITH VARIABLE DIAMETER

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ABSTRACT. We propose a simple graphical approach to steady state solutions of the cable equation for a general model of dendritic tree with tapering. A simple case of transient solutions is also briefly discussed.

1. INTRODUCTION

The function of many physiological systems depends on branched structures that exist both at the tissue (e.g. nervous plexi, lungs, and the vascular and lymphatic systems) and the cellular level (e.g. neurons). Of particular interest, local and global propagation of electrical signals within the nervous system depends on the integration, processing, and further generation of electrical pulses that travel through neurons. In turn, the tree-like morphology of neurons facilitates simultaneous signaling to cells located in different places and over long distances.

Neuronal morphology is typically modeled by assuming that the shape of small neuronal segments, or *neurites*, is approximated by cylinders of different diameters. As a consequence, cable theory [45], [46], [47], [48], [49], [50] plays a central role in the theoretical and experimental study of electrical conduction in neurons; see, for example [8], [11], [59], [14], [19], [20], [21], [22], [23], [31], [53], [57] and references therein. Notably, one of the most interesting results from recent theoretical work is that geometrical properties of neuronal membranes may exert powerful effects on signal propagation even in the presence of voltage-dependent channels [60].

Theoretical research involving realistic neuronal morphologies is typically done by numerically solving systems of cable equations defined on cylinders with different radii, and assuming that voltage and current are continuous functions of space and time. To the best of our knowledge, graphical methods seem have not been widely applied yet in the mathematical modeling of neurons. Graphical methods are very useful and popular in different branches of modern physics. It is worth noting, for example, Feynman diagrams in quantum mechanical or statistical field theory [3], [4], [10], [25], [26], [27], [32], [37], [63], Vilenkin-Kuznetsov-Smorodinskii approach to solutions of n -dimensional Laplace equation [38], [42], [54], [55], applications in solid-state theory, etc. A goal of this paper is to make a modest step in this direction (see also [1], [14] and references therein). We use explicit solutions from recent papers on variable quadratic Hamiltonians in nonrelativistic quantum mechanics [12], [15], [16], [17], [18], [35], [38], [56], [58] to describe steady state and transient solutions to linear cable equations modeling neurites with non-necessarily constant radius.

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2. CABLE EQUATION WITH VARYING RADIUS

At a closer view, neurites can be regarded as volumes of revolution, defined by rotating a smooth function $r = r(x)$ representing the local radius of the neurite where x represents distance along the neurite. As a result, the cable theory implies the following set of equations [31], [47]:

$$2\pi r I_m \frac{ds}{dx} = -\frac{\partial I}{\partial x}, \quad \frac{ds}{dx} = \sqrt{1 + \left(\frac{dr}{dx}\right)^2} \quad (2.1)$$

$$I_m = \frac{V}{R_m} + C_m \frac{\partial V}{\partial t}, \quad (2.2)$$

$$I = -\frac{\pi r^2}{R_i} \frac{\partial V}{\partial x}. \quad (2.3)$$

Here, V represents the voltage difference across the membrane (interior minus exterior) as a deviation from its resting value, I_m is the membrane current density, $I = I_a$ is the total axial current, R_m is the membrane resistance, R_i is the intercellular resistivity and C_m is membrane capacitance (more details can be found in [31], [45] and [47]). Differentiating equation (2.3) with respect to x and substituting the result into (2.1) with the help of (2.2) one gets

$$\left(V + C_m R_m \frac{\partial V}{\partial t}\right) \sqrt{1 + \left(\frac{dr}{dx}\right)^2} = \frac{R_m}{2R_i} \frac{1}{r} \frac{\partial}{\partial x} \left(r^2 \frac{\partial V}{\partial x}\right), \quad (2.4)$$

which is the cable equation with tapering for a single branch of dendritic tree (see [19], [31], [47] and [57] for more details).

We shall be particularly interested in solutions of the cable equation (2.4) corresponding to termination with a “sealed end”, namely, when at the end point $x = x_1$ the membrane cylinder is sealed with a disk composed of the same membrane. In this case, the corresponding boundary condition can be derived by setting

$$I_a = \pi r^2 I_m, \quad (2.5)$$

at $x = x_1$. Then, in view of (2.2)–(2.3), one gets [45]:

$$\left(V + C_m R_m \frac{\partial V}{\partial t} + \frac{R_m}{R_i} \frac{\partial V}{\partial x}\right) \Big|_{x=x_1} = 0, \quad t \geq 0. \quad (2.6)$$

In a similar fashion, at the somatic end one gets

$$\left(V + C_s R_s \frac{\partial V}{\partial t} - \frac{R_s}{R_i} \frac{\partial V}{\partial x}\right) \Big|_{x=x_0} = 0, \quad t \geq 0, \quad (2.7)$$

where R_s is the somatic resistance and C_s is the somatic capacitance [20]. We shall use these conditions for the steady-state and transient solutions of the cable equation. (Later we may impose similar boundary conditions at the points of branching.)

In this Letter, we shall first concentrate on steady-state solutions of the cable equation, when $\partial V / \partial t \equiv 0$. Then

$$V \sqrt{1 + \left(\frac{dr}{dx}\right)^2} = \frac{R_m}{2r R_i} \frac{d}{dx} \left(r^2 \frac{dV}{dx}\right) \quad (x_0 \leq x \leq x_1) \quad (2.8)$$

and

$$V|_{x=x_0} = V_0, \quad \left(\frac{dV}{dx} + B(x)V \right) \Big|_{x=x_1} = 0, \quad B(x_1) = \frac{R_i}{R_m}. \quad (2.9)$$

This boundary value problem can be conveniently solved (by a direct substitution for each branch of the dendritic tree) in terms of standard solutions of this second order ordinary differential equation as follows

$$V(x) = V(x_0) \frac{C(x) + B(x_1)S(x)}{C(x_0) + B(x_1)S(x_0)}, \quad (2.10)$$

where $C(x)$ and $S(x)$ are two linearly independent solutions of the stationary cable equation (2.8) that satisfy special boundary conditions $C(x_1) = 1$, $C'(x_1) = 0$ and $S(x_1) = 0$, $S'(x_1) = -1$. Then

$$\frac{dV}{dx} + B(x)V = 0 \quad (x_0 \leq x \leq x_1) \quad (2.11)$$

with the corresponding current density/voltage ratio function $B(x)$ given by

$$B(x) = -\frac{V'}{V} = -\frac{C'(x) + B(x_1)S'(x)}{C(x) + B(x_1)S(x)} \quad (2.12)$$

in term of the standard solutions $C(x)$ and $S(x)$. Throughout this Letter, we shall refer to a case, when $B(x) > 0$ ($x_0 < x < x_1$), as the case of weak tapering. An opposite situation, when $B(\xi) = 0$ at certain point $x_0 < \xi < x_1$ and an inverse of the current may occur, shall be called a case of the strong tapering. (A case of strong tapering has been numerically discovered in [28].)

3. TAPERING WITH ANALYTIC, ASYMPTOTIC AND/OR NUMERICAL SOLUTIONS

In this Letter, we consider a general model of a dendrite as a (binary) directed tree (from the soma to its terminal ends) consisting of axially symmetric branches with the following types of tapering.

3.1. Cylinder. Here, $r = r_0 = \text{constant}$, $0 \leq x \leq L$ and the cable equation takes the simplest form

$$\lambda^2 \frac{d^2 V}{dx^2} = V, \quad \lambda^2 = \frac{r_0 R_m}{2R_i} \quad (3.1)$$

with a familiar solution [31], [45], [47]:

$$V(x) = V_0 \frac{\cosh((L-x)/\lambda) + \lambda B_L \sinh((L-x)/\lambda)}{\cosh(L/\lambda) + \lambda B_L \sinh(L/\lambda)} \quad (3.2)$$

subject to boundary conditions

$$V(0) = V_0, \quad B_L V(L) + \frac{dV}{dx}(L) = 0. \quad (3.3)$$

Then

$$B(x) = \frac{\lambda B_L + \tanh((L-x)/\lambda)}{\lambda + \lambda^2 B_L \tanh((L-x)/\lambda)}. \quad (3.4)$$

(See [31], [47], [49], [50], [59] and references therein for more details.)

3.2. Frustum(Cone). Here, $r = r(x) = r_0 + \frac{r_1 - r_0}{L}x$ with $0 \leq x \leq L$. The steady-state solution of the corresponding cable equation

$$r \frac{d^2 V}{dx^2} + 2 \frac{dV}{dx} = \frac{\mu^2}{4} V, \quad \mu = \sqrt{\frac{8R_i}{R_m} \left(1 + \left(\frac{r_1 - r_0}{L}\right)^2\right)^{1/4}} \quad (3.5)$$

subject to boundary conditions (3.3) are given by [7]

$$V(x) = V_0 \frac{C(L-x) + B_L S(L-x)}{C(L) + B_L S(L)}. \quad (3.6)$$

Here, the standard solutions that satisfy $S(0) = 0$, $S'(0) = 1$ and $C(0) = 1$, $C'(0) = 0$ can be constructed as follows

$$S(x) = \frac{2Lr_0^{3/2}}{(r_1 - r_0)\sqrt{r}} [K_1(\mu\sqrt{r_0}) I_1(\mu\sqrt{r}) - I_1(\mu\sqrt{r_0}) K_1(\mu\sqrt{r})] \quad (3.7)$$

and

$$\begin{aligned} C(x) = & [\mu\sqrt{r_0} K_0(\mu\sqrt{r_0}) + 2K_1(\mu\sqrt{r_0})] \sqrt{\frac{r_0}{r_1}} I_1(\mu\sqrt{r}) \\ & + [\mu\sqrt{r_0} I_0(\mu\sqrt{r_0}) - 2I_1(\mu\sqrt{r_0})] \sqrt{\frac{r_0}{r_1}} K_1(\mu\sqrt{r}) \end{aligned} \quad (3.8)$$

in terms of modified Bessel functions $I_\nu(z)$ and $K_\nu(z)$ of orders $\nu = 0, 1$ (different aspects of the advanced theory of Bessel functions can be found in [2], [5], [6], [24], [41], [43], [44], [61] and [62]).

3.3. Hyperbola. If $r = a \cosh\left(\frac{x-b}{a}\right)$ on an interval $x_0 \leq x \leq x_1$, the cable equation (2.4) takes the form

$$\left(V + C_m R_m \frac{\partial V}{\partial t}\right) \cosh\left(\frac{x-b}{a}\right) = \frac{R_m}{2R_i} \left[2 \sinh\left(\frac{x-b}{a}\right) \frac{\partial V}{\partial x} + a \cosh\left(\frac{x-b}{a}\right) \frac{\partial^2 V}{\partial x^2}\right]. \quad (3.9)$$

This special case of tapering is integrable in terms of elementary functions [30] (see also [12] and [17] for a similar problem related to a model of the damped quantum oscillator). For the steady-state solutions one obtains the following equation

$$V'' + 2\lambda \tanh(\lambda x + \delta) V' = \mu_0^2 V \quad (3.10)$$

with new parameters

$$\lambda = \frac{1}{a}, \quad \delta = -\lambda b, \quad \mu_0^2 = \frac{2R_i}{aR_m}. \quad (3.11)$$

The corresponding two linearly independent solutions, namely,

$$V_1(x) = \frac{\sinh(\mu x + \gamma)}{\cosh(\lambda x + \delta)}, \quad V_2(x) = \frac{\cosh(\mu x + \gamma)}{\cosh(\lambda x + \delta)}, \quad \mu = \sqrt{\mu_0^2 + \lambda^2}, \quad (3.12)$$

can be verified by a direct substitution for an arbitrary parameter γ .

The required steady-state solution of the boundary value problem

$$V(x_0) = V_0, \quad BV(x_1) + \frac{dV}{dx}(x_1) = 0 \quad (3.13)$$

is given by

$$V(x) = V_0 \frac{C(x_1 - x) + BS(x_1 - x)}{C(x_1 - x_0) + BS(x_1 - x_0)}, \quad (3.14)$$

where

$$\begin{aligned} C(x_1 - x) &= \cosh(\lambda(b - x_1)) \frac{\cosh(\mu(x_1 - x))}{\cosh(\lambda(x - b))} \\ &\quad + \sinh(\lambda(b - x_1)) \frac{\lambda \sinh(\mu(x_1 - x))}{\mu \cosh(\lambda(x - b))} \end{aligned} \quad (3.15)$$

and

$$S(x_1 - x) = \cosh(\lambda(b - x_1)) \frac{\sinh(\mu(x_1 - x))}{\mu \cosh(\lambda(x - b))}. \quad (3.16)$$

(See [30] for more details.)

3.4. General Case of Axial Symmetry. One can use numerical methods and/or WKB-type approximation in order to obtain standard solutions. For example [41],

$$V \approx \frac{1}{\sqrt{r^2(x)p(x)}} [Ae^{\xi(x)} + Be^{-\xi(x)}], \quad (3.17)$$

where

$$p(x) = \left(\frac{2}{r} \frac{ds}{dx} \frac{R_i}{R_m} \right)^{1/2}, \quad \xi(x) = \int_{x_0}^x p(t) dt. \quad (3.18)$$

(See [31] and [47] for further details.)

4. A GRAPHICAL APPROACH

Graphical rules for steady-state voltages and currents in a model of dendritic tree with tapering are as follows.

4.1. Single Axially Symmetric Branch with Arbitrary Tapering. For a single branch with tapering voltage and current density/voltage ratio are given by

$$V(x) = \frac{C(x_1 - x) + B(x_1)S(x_1 - x)}{C(x_1 - x_0) + B(x_1)S(x_1 - x_0)} V(x_0) \quad (4.1)$$

$$= (C(x_1 - x) + B(x_1)S(x_1 - x)) V(x_1),$$

$$B(x) = \frac{C'(x_1 - x) + B(x_1)S'(x_1 - x)}{C(x_1 - x) + B(x_1)S(x_1 - x)} = -\frac{V'(x)}{V(x)}, \quad (4.2)$$

respectively (see Figure 1).

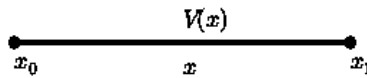


FIGURE 1. A Single Branch with Tapering.

4.2. Junction of Three Branches with Different Types of Tapering. The internal potential and current are assumed to be continuous at all dendritic branch points and at the soma-dendritic junction [45]. We consider a general case when each branch has its own tapering, say $r = r(x)$, $r_1 = r_1(x)$ and $r_2 = r_2(x)$ (see Figure 2). Then

$$V(x_{12}) = V_1(x_{12}) = V_2(x_{12}), \quad (4.3)$$

$$r^2(x_{12}) B(x_{12}) = r_1^2(x_{12}) B_1(x_{12}) + r_2^2(x_{12}) B_2(x_{12}). \quad (4.4)$$

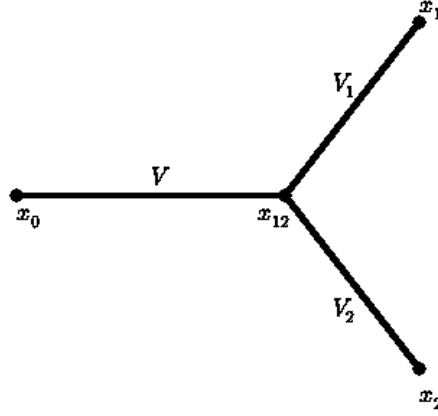


FIGURE 2. A Junction of Three Different Branches.

The total ratio constant $B(x_{12})$ at the branching point x_{12} is given by the following expression

$$\begin{aligned} B(x_{12}) &= \frac{r_1^2(x_{12})}{r^2(x_{12})} B_1(x_{12}) + \frac{r_2^2(x_{12})}{r^2(x_{12})} B_2(x_{12}) \\ &= B(B_1(x_1), B_2(x_2)) \\ &= \frac{r_1^2(x_{12}) \frac{C'_1(x_1 - x_{12})}{C_1(x_1 - x_{12})} + B_1(x_1) \frac{S'_1(x_1 - x_{12})}{S_1(x_1 - x_{12})}}{r^2(x_{12}) \frac{C'_1(x_1 - x_{12})}{C_1(x_1 - x_{12})} + B_1(x_1) \frac{S'_1(x_1 - x_{12})}{S_1(x_1 - x_{12})}} \\ &\quad + \frac{r_2^2(x_{12}) \frac{C'_2(x_2 - x_{12})}{C_2(x_2 - x_{12})} + B_2(x_2) \frac{S'_2(x_2 - x_{12})}{S_2(x_2 - x_{12})}}{r^2(x_{12}) \frac{C'_2(x_2 - x_{12})}{C_2(x_2 - x_{12})} + B_2(x_2) \frac{S'_2(x_2 - x_{12})}{S_2(x_2 - x_{12})}}. \end{aligned} \quad (4.5)$$

Then the ratio constant $B(x_0)$ is

$$B(x_0) = \frac{C'(x_{12} - x_0) + B(x_{12}) S'(x_{12} - x_0)}{C(x_{12} - x_0) + B(x_{12}) S(x_{12} - x_0)} \quad (4.6)$$

with the coefficient $B(x_{12})$ found by the previous formula (4.5).

4.3. Junction of $(n + 1)$ -Branches. In a similar fashion, at the branching point x_α , one gets

$$V(x_\alpha) = V_1(x_\alpha) = V_2(x_\alpha) = \dots = V_n(x_\alpha), \quad (4.7)$$

$$\begin{aligned} r^2(x_\alpha) B(x_\alpha) &= r_1^2(x_\alpha) B_1(x_\alpha) + r_2^2(x_\alpha) B_2(x_\alpha) + \dots + r_n^2(x_\alpha) B_n(x_\alpha) \\ &= \sum_{i=1}^n r_i^2(x_\alpha) B_i(x_\alpha). \end{aligned} \quad (4.8)$$

(See Figure 3.)

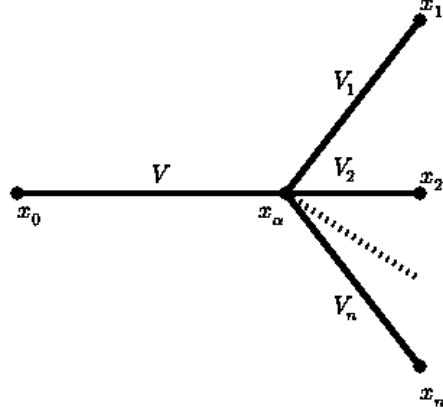


FIGURE 3. A Junction of $(n + 1)$ -Branches.

Combination of the above graphical rules results in a simple algorithm of evaluation of voltages and currents in the model of dendritic tree under consideration as follows.

Evaluate constants $B(x_\alpha)$ for all branching points of the tree: (a) first apply formula (4.5) for all open notes; (b) remove the above nodes from the tree and keep repeating the previous step until you reach the root of tree (soma).

In order to find voltage at a point x of the dendritic tree, follow the path $x_0 \rightarrow x$ and multiply the initial voltage $V(x_0)$ by consecutive corresponding factors from formula (4.1) changing at each intersection of the tree. The ratio of voltages $V(x_\alpha)$ and $V(x_\beta)$ at two terminal points, can be determine in a graphic form by the previous rule applied to the shortest path $x_\beta \rightarrow x_\beta$.

5. EXAMPLES

Our formulas (4.5)–(4.6) define ratio coefficients $B(x_\alpha)$ for all vertexes for the standard node on Figure 2. For the corresponding voltages, one can write

$$\begin{aligned}
 V(x_0) &= [C(x_{12} - x_0) + B(x_{12}) S(x_{12} - x_0)] V(x_{12}) \\
 &= [C(x_{12} - x_0) + B(x_{12}) S(x_{12} - x_0)] V(x_{12}) \\
 &\quad \times [C(x_1 - x_{12}) + B(x_1) S(x_1 - x_{12})] V(x_1) \\
 &= [C(x_{12} - x_0) + B(x_{12}) S(x_{12} - x_0)] V(x_{12}) \\
 &\quad \times [C(x_2 - x_{12}) + B(x_2) S(x_2 - x_{12})] V(x_2)
 \end{aligned} \tag{5.1}$$

and

$$\frac{V(x_1)}{V(x_2)} = \frac{C(x_2 - x_{12}) + B(x_2) S(x_2 - x_{12})}{C(x_1 - x_{12}) + B(x_1) S(x_1 - x_{12})}. \tag{5.2}$$

Further examples are left to the reader.

6. TRANSIENT SOLUTIONS

6.1. A Single Branch with Smooth Tapering. Let us consider the cable equation (2.4) for a single branch with an arbitrary smooth tapering $r = r(x)$ on the interval $x_0 \leq x \leq x_1$. The separation of variables

$$V(x, t) = e^{-(1+\alpha^2)t/\tau_m} U(x), \quad \tau_m = C_m R_m \quad (6.1)$$

in results in

$$\frac{1}{r} \frac{d}{dx} \left(r^2 \frac{dU}{dx} \right) + \omega^2 \frac{ds}{dx} U = 0, \quad \omega^2 = \frac{2R_i}{R_m} \alpha^2, \quad (6.2)$$

where α is a separation constant. The boundary condition at the sealed end (2.6) takes the form

$$\left(\frac{dU}{dx} - \frac{1}{2} \omega^2 U \right) \Big|_{x=x_1} = 0. \quad (6.3)$$

A general solution of this problem can be conveniently written (for each branch of the dendritic tree) as follows

$$U(x) = U(x, \omega) = A \left[C(x, \omega) + \frac{1}{2} \omega^2 S(x, \omega) \right], \quad (6.4)$$

where A is a constant and $C(x, \omega)$ and $S(x, \omega)$ are two linearly independent standard solutions of equation (6.2) that satisfy special boundary conditions $C(x_1, \omega) = 1$, $C'(x_1, \omega) = 0$ and $S(x_1, \omega) = 0$, $S'(x_1, \omega) = 1$. Then the boundary condition (2.7) at the somatic end $x = x_0$, namely,

$$\left(\frac{dU}{dx} + \left[\frac{R_i}{R_s} \left(\frac{\tau_s}{\tau_m} - 1 \right) + \frac{C_s}{2C_m} \omega^2 \right] U \right) \Big|_{x=x_0} = 0, \quad \tau_s = C_s R_s, \quad (6.5)$$

results in a transcendental equation

$$\left[1 - \frac{\tau_s}{\tau_m} \left(1 + \frac{R_m}{2R_i} \omega^2 \right) \right] \frac{R_i}{R_s} = \frac{C'(x_0, \omega) + \frac{1}{2} \omega^2 S'(x_0, \omega)}{C(x_0, \omega) + \frac{1}{2} \omega^2 S(x_0, \omega)} \quad (6.6)$$

for the eigenvalues ω . (There are infinitely many discrete eigenvalues [13] and [29], Ince?.) The corresponding eigenfunctions $U_n = U(x, \omega_n) = A_n u_n(x)$ are orthogonal

$$(u_m, u_n) = \delta_{mn} (u_n, u_n) \quad (6.7)$$

with respect to an inner product that is given in terms of the Lebesgue–Stieltjes integral [13] (see also Appendix and [33], [51] and [52]):

$$\begin{aligned} (u, v) : &= \int_{x_0}^{x_1} u(x) v(x) r(x) ds \\ &+ \frac{1}{2} r^2(x_1) u(x_1) v(x_1) + \frac{C_s}{2C_m} r^2(x_0) u(x_0) v(x_0). \end{aligned} \quad (6.8)$$

A formal solution of the corresponding initial value problem takes the form

$$\begin{aligned} V(x, t) &= V(x, \infty) \\ &+ \sum_n A_n \exp \left[- \left(1 + \frac{R_m}{2R_i} \omega_n^2 \right) \frac{t}{\tau_m} \right] u_n(x), \end{aligned} \quad (6.9)$$

where $V(x, \infty)$ is the steady-state solution, $\omega = \omega_n$ are roots of the transcendental equation (6.6) and the corresponding eigenfunctions are given by

$$u_n(x) = C(x, \omega_n) + \frac{1}{2}\omega_n^2 S(x, \omega_n). \quad (6.10)$$

Coefficients A_n can be obtained by methods of Refs. [13] and [20] with the help of the modified orthogonality relation (6.7) as follows

$$A_n = \frac{(V(x, 0) - V(x, \infty), u_n(x))}{(u_n(x), u_n(x))}. \quad (6.11)$$

Substitution of (6.11) into (6.9) and changing the order of summation and integration result in

$$\begin{aligned} V(x, t) &= V(x, \infty) \\ &+ \int_{\text{Supp } \mu} G(x, y, t) (V(y, 0) - V(y, \infty)) d\mu(y), \end{aligned} \quad (6.12)$$

where

$$G(x, y, t) = \sum_n \exp \left[- \left(1 + \frac{R_m}{2R_i} \omega_n^2 \right) \frac{t}{\tau_m} \right] \frac{u_n(x) u_n(y)}{\|u_n\|^2} \quad (6.13)$$

is an analog of the heat kernel. Infinite speed of propagation. Method of images.

6.2. A Single Branch with Piecewise Typing. In the case of a piecewise tapering

$$r = \begin{cases} r_0(x), & x_0 \leq x \leq x_{01} \\ r_1(x), & x_{01} \leq x \leq x_1 \end{cases} \quad (6.14)$$

with $r_0(x_{01}^-) = r_1(x_{01}^+)$, in a similar fashion, one can write

$$U(x, \omega) = \begin{cases} A_0 \left[C_0(x, \omega) - \left(\frac{R_i}{R_s} \left(\frac{\tau_s}{\tau_m} - 1 \right) + \frac{C_s}{2C_m} \omega^2 \right) S_0(x, \omega) \right], & x_0 \leq x \leq x_{01} \\ A_1 \left[C_1(x, \omega) + \frac{1}{2} \omega^2 S_1(x, \omega) \right], & x_{01} \leq x \leq x_1 \end{cases} \quad (6.15)$$

provided $C_0(x_0, \omega) = 1$, $C'_0(x_0, \omega) = 0$ and $S_0(x_0, \omega) = 0$, $S'_0(x_0, \omega) = 1$ and $C_1(x_1, \omega) = 1$, $C'_1(x_1, \omega) = 0$ and $S_1(x_1, \omega) = 0$, $S'_1(x_1, \omega) = 1$. Continuity and smoothness of the solution at the point x_{01} , namely,

$$\frac{U'(x_{01}^-)}{U(x_{01}^-)} = \frac{U'(x_{01}^+)}{U(x_{01}^+)}, \quad (6.16)$$

results in the following equation for the eigenvalues

$$\frac{C'_0(x_{01}, \omega) - \left(\frac{R_i}{R_s} \left(\frac{\tau_s}{\tau_m} - 1 \right) + \frac{C_s}{2C_m} \omega^2 \right) S'_0(x_{01}, \omega)}{C_0(x_{01}, \omega) - \left(\frac{R_i}{R_s} \left(\frac{\tau_s}{\tau_m} - 1 \right) + \frac{C_s}{2C_m} \omega^2 \right) S_0(x_{01}, \omega)} = \frac{C'_1(x_{01}, \omega) + \frac{1}{2} \omega^2 S'_1(x_{01}, \omega)}{C_1(x_{01}, \omega) + \frac{1}{2} \omega^2 S_1(x_{01}, \omega)}. \quad (6.17)$$

Introducing

$$u_n(x) = \begin{cases} u_n^{(0)}(x) / u_n^{(0)}(x_{01}), & x_0 \leq x \leq x_{01} \\ u_n^{(1)}(x) / u_n^{(1)}(x_{01}), & x_{01} \leq x \leq x_1 \end{cases}, \quad (6.18)$$

where

$$u_n^{(0)}(x) = C_0(x, \omega_n) - \left(\frac{R_i}{R_s} \left(\frac{\tau_s}{\tau_m} - 1 \right) + \frac{C_s}{2C_m} \omega_n^2 \right) S_0(x, \omega_n),$$

$$u_n^{(1)}(x) = C_1(x, \omega_n) + \frac{1}{2}\omega^2 S_1(x, \omega_n),$$

one can obtain a formal solution in the form (6.12)–(6.13) once again. Further details are left to the reader.

7. SUMMARY

In this Letter, we propose a simple graphical approach to steady state solutions of the cable equation for a general model of dendritic tree with tapering. A simple case of transient solutions is also briefly discussed.

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APPENDIX A. MODIFIED ORTHOGONALITY RELATION

We consider the Sturm–Liouville type problem,

$$Lu + \lambda \rho u = 0, \tag{A.1}$$

for the second order differential operator

$$Lu = \frac{d}{dx} \left[k(x) \frac{du}{dx} \right] - q(x) u, \tag{A.2}$$

where k , q and ρ are continuous real-valued functions on an interval $[x_0, x_1]$, k and ρ are positive in $[x_0, x_1]$, k' exists and is continuous in $[x_0, x_1]$, subject to modified boundary conditions

$$\begin{aligned} u'(x_0) + (a_0 + b_0 \lambda) u(x_0) &= 0, \\ u'(x_1) + (a_1 - b_1 \lambda) u(x_1) &= 0, \end{aligned} \tag{A.3}$$

where $a_0, b_0 \geq 0$ and $a_1, b_1 \geq 0$ are constants. With the help of the second Green's formula (see, for example, [40]),

$$\int_{x_0}^{x_1} (vLu - uLv) dx = k \left(v \frac{du}{dx} - u \frac{dv}{dx} \right) \Big|_{x_0}^{x_1}, \tag{A.4}$$

for two eigenfunctions u and v corresponding to different eigenvalues

$$Lu + \lambda \rho u = 0, \quad Lv + \mu \rho v = 0, \quad \lambda \neq \mu \tag{A.5}$$

one gets the following orthogonality relation [13]:

$$\int_{x_0}^{x_1} u(x) v(x) \rho dx + b_1 k(x_1) u(x_1) v(x_1) + b_0 k(x_0) u(x_0) v(x_0) = 0. \tag{A.6}$$

Here, the modified inner product

$$(u, v) \quad : \quad = \int_{\text{Supp } \mu} uv d\mu \tag{A.7}$$

$$= \int_{x_0}^{x_1} u(x) v(x) \rho dx + b_1 k(x_1) u(x_1) v(x_1) + b_0 k(x_0) u(x_0) v(x_0)$$

is defined in terms of the Lebesgue–Stieltjes integral [34]. The modified orthogonality relation (A.6) holds also in the case of a piecewise continuous derivative k' on the interval $[x_0, x_1]$.

The junction of three branches (see Figure 2) can be considered in a similar fashion. Suppose that

$$L_i u_i + \lambda \rho_i u_i = 0, \quad L_i u = \frac{d}{dx} \left[k_i(x) \frac{du}{dx} \right] - q_i(x) u \quad (\text{A.8})$$

with $k = 0, 1, 2$ for three corresponding branches, respectively, and boundary conditions are given by

$$\begin{aligned} u'(x_0) + (a_0 + b_0 \lambda) u(x_0) &= 0, \\ u'(x_1) + (a_1 - b_1 \lambda) u(x_1) &= 0, \\ u'(x_2) + (a_2 - b_2 \lambda) u(x_2) &= 0 \end{aligned} \quad (\text{A.9})$$

at the terminal ends. Introducing integration over the whole tree T by additivity,

$$\begin{aligned} \int_T (vLu - uLv) dx &= \int_{x_0}^{x_1} (v_0 L_0 u_0 - u_0 L_0 v_0) dx \\ &+ \int_{x_{12}}^{x_1} (v_1 L_1 u_1 - u_1 L_1 v_1) dx + \int_{x_{12}}^{x_2} (v_2 L_2 u_2 - u_2 L_2 v_2) dx, \end{aligned} \quad (\text{A.10})$$

and applying the Green formula (A.4) for each branch, one gets

$$\begin{aligned} \int_T (vLu - uLv) dx &= k_0(x_{12}) (v_0(x_{12}) u'_0(x_{12}) - u_0(x_{12}) v'_0(x_{12})) \\ &- k_1(x_{12}) (v_1(x_{12}) u'_1(x_{12}) - u_1(x_{12}) v'_1(x_{12})) \\ &- k_2(x_{12}) (v_2(x_{12}) u'_2(x_{12}) - u_2(x_{12}) v'_2(x_{12})) \\ &- k_0(x_0) (v_0(x_0) u'_0(x_0) - u_0(x_0) v'_0(x_0)) \\ &+ k_1(x_1) (v_1(x_1) u'_1(x_1) - u_1(x_1) v'_1(x_1)) \\ &+ k_2(x_2) (v_2(x_2) u'_2(x_2) - u_2(x_2) v'_2(x_2)). \end{aligned} \quad (\text{A.11})$$

We shall assume that the following continuity conditions:

$$\begin{aligned} u_0(x_{12}) &= u_1(x_{12}) = u_2(x_{12}), \\ k_0(x_{12}) u'_0(x_{12}) &= k_1(x_{12}) u'_1(x_{12}) = k_2(x_{12}) u'_2(x_{12}) \end{aligned} \quad (\text{A.12})$$

hold at the branching point x_{12} . In view of the boundary conditions (A.9), the modified orthogonality relation takes the form

$$\begin{aligned} \int_{x_0}^{x_1} u(x) v(x) \rho dx + \int_{x_0}^{x_1} u(x) v(x) \rho dx + \int_{x_0}^{x_1} u(x) v(x) \rho dx \\ + b_0 k(x_0) u(x_0) v(x_0) + b_1 k(x_1) u(x_1) v(x_1) + b_2 k(x_2) u(x_2) v(x_2) = 0. \end{aligned} \quad (\text{A.13})$$

The case of junction of $(n+1)$ -branches (see Figure 3) is similar. In general, for an arbitrary tree, one may conclude that only the terminal ends shall add additional mass points to the measure, if the corresponding boundary and continuity conditions hold. Further details are left to the reader.

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